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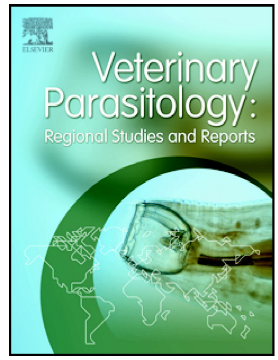

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Gastrointestinal parasites in reindeer (*Rangifer tarandus tarandus*): a review focusing on Fennoscandia

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Abstract

Reindeer (*Rangifer tarandus tarandus*) are known to host a wide variety of parasites, including those in the gastrointestinal system. Here, we review the current knowledge of the main gastrointestinal parasites of reindeer focusing on northern Fennoscandia, which comprises parts of Finland, Sweden, Norway and Russia. We explore both the historical baseline data for diversity and distribution and recent advancements in our understanding of parasite faunas in reindeer across this region. It is evident that the balance between reindeer and their gastrointestinal parasites, along with the potential for emergent disease in the changing world warrants careful monitoring and further studies.

Keywords

reindeer; gastrointestinal parasites; Fennoscandia; protozoa; nematodes; cestodes

1. Introduction

In northern Fennoscandia, comprising parts of Finland, Sweden, Norway, and Russia, reindeer (*Rangifer tarandus tarandus*) are semidomesticated animals that graze freely on natural pastures most of the year. Geographically, reindeer husbandry is relatively stationary in Finland (Horstkotte and Aikio, 2017), while seasonal migration between summer and winter grazing grounds is typical in Sweden and Norway.

Reindeer have a high prevalence of subclinical, low-intensity mixed gastrointestinal parasitic infections (Halvorsen, 1986; Oksanen, 1999; Hoberg et al., 2001; Hrabok, 2006; Laaksonen et al., 2008; Josefsen et al., 2014; Laaksonen, 2016; Laaksonen et al., 2017; Tryland and Kutz, 2018; Jokelainen et al., 2019). The balance between reindeer and their parasites is subject to changes that are directly influenced by their husbandry, local or landscape factors of geography and climate. In Finnish reindeer husbandry, ivermectin is administrated annually to a large proportion of breeding reindeer (Jokelainen et al., 2019). Most recently, the advent of anthelmintic and antiparasitic resistance may directly influence population persistence, and changing patterns of abundance and prevalence.

Here, we review the current knowledge of selected gastrointestinal parasites of reindeer with a focus on Fennoscandia and discuss needs for monitoring and research in the near future coincidental with changing management practices and environmental perturbations. The parasites included in this review can be detected in feces of reindeer using flotation methods and microscopy.

2 Gastrointestinal parasites of reindeer

2.1 Gastrointestinal protozoa

Eimeria spp.

Coccidians of the genus *Eimeria* are the most common and important gastrointestinal protozoa in young domestic animals (Soulsby, 1983) and they also play a relevant role in reindeer. These parasites live in the mucosal or lamina propria cells of the intestine and have a direct lifecycle. Oocysts (Fig. 1, F) are shed in the host feces. Sporulated oocysts may survive up to two weeks at temperatures of –12 to –20 °C in the environment (Soulsby, 1983), are capable of overwintering in Fennoscandian conditions, and can infect calves in the subsequent spring (Svensson, 1995).

Each cycle results in destruction of intestinal cells and may cause clinical disease (Dau, 1981; Soulsby, 1983).

In reindeer a minimum 8 species have been described: *Eimeria arctica* (Yakimoff et al., 1939), *E. mayeri* (Yakimoff et al., 1936), *E. mühlensi* (Yakimoff et al., 1936), *E. tarandina* (Yakimoff et al., 1936), and *Isospora rangiferis* (Yakimoff et al., 1936; Yakimoff et al., 1937; Yakimoff et al., 1939; Pellérdy, 1974), *E. rangiferis* (Gudmundsdóttir and Skirnisson, 2005), *E. hreindyria* (Gudmundsdóttir and Skirnisson, 2006) reviewed by Skirnisson and Cuyler (2016) and *E. tuttui* (Skirnisson and Cuyler, 2016). In Fennoscandia, unidentified oocysts attributed to species of *Eimeria* have been reported in 22% of adult Finnish reindeer (Nikander, 1986) and from Sweden (Christensson and Rehbinder, 1975). Although prevalence in wild adult reindeer is generally low, *Eimeria* sp. are common in semidomesticated reindeer calves. In Finland, a high prevalence of coccidia (35%), and often a high intensity of the infection, was observed in 494 reindeer calves (Oksanen et al., 1990). In a more recent study, *Eimeria* sp. prevalence was 48% in 115 reindeer calves (Laaksonen et al., 2008), and in the most recent study, *Eimeria* sp. prevalence was 51% among 460 reindeer calves (Jokelainen et al., 2019). Higher reindeer density has been identified as a risk factor for reindeer calves shedding *Eimeria* sp. oocysts (Jokelainen et al., 2019).

In cervids, even heavy infection with *Eimeria* spp. can be subclinical (Conloque and Foreyt, 1984; Foreyt and Lagerquist, 1994). In weakened young fawns, infection can however lead to serious gastroenteritis (Abbas and Post, 1980). Moderate infections in reindeer are usually subclinical (Christensson and Rehbinder, 1975). Because each coccidian oocyst destroys at least one epithelial cell when emerging to the intestine lumen, the peak fecal oocyst counts, up to

800000 opg (oocysts per gram), cannot be considered to represent benign infection (Oksanen et al., 1990).

2.2 Gastrointestinal nematodes

Gastrointestinal nematodes that typically parasitize reindeer all have direct life cycles. Eggs of strongylid nematodes are shed on pasture within the feces. A first-stage larva (L1) hatches from the egg and moults twice to become an infective third-stage larva (L3) (reviewed by Hrabok, 2006). In the case of the subfamily Nematodirinae, the development of the L3 occurs within the egg and thereafter the egg hatches, releasing the infective larva on pasture. Strongylid larvae and *Capillaria*, *Trichuris* and *Skrjabinema* eggs containing infective larvae are transmitted via the intake of vegetation. The pre-parasitic infective L3 stages of strongyles can withstand the harsh climatic conditions in the environment of the Arctic, and parasite transmission occurs continuously throughout the year for nematode parasites of reindeer (Halvorsen et al., 1999).

Strongylids

Among the gastrointestinal strongyles, or strongylids, those of the abomasum are considered the most important production limiting parasites of ruminants (Sykes, 1987; Fruetel and Lancaster, 1988). The dominant species in reindeer is *Ostertagia gruehneri* along with its minor morphotype, *O. arctica* (Bye and Halvorsen, 1983; Bye, 1987; Nikander, 1988; Halvorsen et al., 1999; Hrabok, 2006; Kutz et al., 2012). It is important to note that all of the ostertagiine nematodes, including species of *Ostertagia*, *Marshallagia* and *Teladorsagia* that occur in ruminants from the Arctic are polymorphic, and are represented by two or three discrete males depending on the genus, with one morphotype (termed the “major”) that is usually dominant in an infection (e.g., Lichtenfels and Pilitt, 1989; Hoberg et al., 1999, 2012). This phenomenon has confounded identification, and most particularly has led to some erroneous reports in the literature when species diversity is documented (e.g., Hoberg et al., 2012).

Among the ostertagiines, eggs passed in feces develop into infective-stage larvae (L3) often in 3–4 weeks, but the rate of development is temperature dependent (Hoar et al., 2012). Freeze tolerance of *O. gruehneri* eggs is unknown, but eggs of the related ostertagiine *Marshallagia marshalli* in the High Arctic Svalbard reindeer survive prolonged freezing (Carlsson et al., 2013). Although eggs of ostertagiines and most gastrointestinal strongyles are morphologically similar (Fig. 1, A), those of *Marshallagia* sp. can be immediately distinguished by large dimensions.

Once acquired by the host while grazing, the L3 moult to the fourth-stage (L4) in the abomasal mucosa before developing into adult worms. The time (prepatent period) between ingestion of the L3 and development to the egg producing adult stage can be as short as 21 days (Halvorsen et al., 1999). In Finland, *O. gruehneri* appears to maintain an annual cycle, and infected calves are shedding parasite eggs already by midsummer and the end of the first summer, which may be associated with type I ostertagiosis (Oksanen et al., 1990; Hrabok, 2006; Laaksonen et al., 2008; Manninen et al., 2014; Jokelainen et al., 2019). A second developmental pathway of these parasites, which tends to occur when L3 are ingested late in the summer, is to overwinter in a hypobiotic state in the mucosa of the abomasum. Maturation and emergence from the mucosa the following spring leads to the syndrome known as type II ostertagiosis (Armour and Duncan, 1987; Hoar et al., 2012; Kutz et al., 2012). Among nematodes derived from either pathway, egg output generally peaks in mid-summer (Irvine et al., 2000; Stien et al., 2002b; Hoar et al., 2009) or in late summer-autumn (Hrabok et al., 2006). Although much of the published information regarding abomasal nematodes is for domestic livestock, infection with *O. gruehneri* has been associated with decreased food intake (Arneberg et al., 1996) and reduction in body condition and fecundity in reindeer (Stien et al., 2002a; Hughes et al., 2009; Steele, 2013). Ostertagiosis may result in substantial inflammation, hemorrhage, edema, and protein and blood loss especially in the heavily infected bovine calves in their second winter before the immunity against *Ostertagia* sp. has developed (Lloyd and Soulsby, 1987; Klesius, 1993). This syndrome is also suspected to occur in reindeer (Rehbinder and von Szokolay, 1978).

Models have demonstrated that the fitness impact of *O. gruehneri* (and its minor male morphotype *O. arctica*) is significant enough to play a role in regulating the population dynamics of Svalbard reindeer (Albon et al., 2002; Carlsson et al., 2016). There are also reports of a broader assemblage of trichostrongylids in reindeer, especially other polymorphic species of ostertagiines: *O. leptospicularis* (and the minor male morphotype *O. kolchida*), *O. ostertagi* (and *O. lyrata*), *Teladorsagia circumcincta* (*T. trifurcata* and *T. davtiani*), and *Marshallagia marshalli* (and *M. occidentalis*) (Rehbinder and Christensson, 1977; Rehbinder and von Szokolay, 1978; Bye and Halvorsen, 1983; Bye, 1987; see Drózdz (1995) and Hoberg et al. (1999, 2012) for discussions of taxonomy among the ostertagiines).

Marshallagia marshalli is typical in wild Svalbard reindeer (Bye et al., 1987), but has not been reported in Fennoscandia among reindeer. *Haemonchus contortus* has been reported to infect Russian reindeer (Pryadko, 1976). Many species, listed above, that principally parasitize other cervids or domestic ruminants, have been found as abomasal nematodes in reindeer (Oksanen, 1999; Hrabok, 2006; Kutz et al., 2012) and *O. gruehneri* has been reported in sheep sharing the same pastures with reindeer (Manninen et al., 2014).

Historically, levels of abundance and prevalence of strongyles in reindeer has been low to moderate. This observation contrasts with current abundance of strongylids (as demonstrated by proportion shedding eggs) which was significantly higher among reindeer calves in the most recent study (Jokelainen et al., 2019) relative to baselines established a decade earlier (Laaksonen et al., 2008). In the most recent study, more than 75% of the reindeer calves examined were demonstrated to shed strongylid eggs (Jokelainen et al., 2019).

Nematodirus/Nematodirella

Nematodirines, *Nematodirella longissemispiculata (=N. longispiculata)* and *Nematodirus tarandi* tend to dwell in the small intestines primarily in young reindeer (Bye, 1987; Fruetel and Lankester, 1989; Oksanen et al., 1990; Hrabok et al., 2007; Kutz et al., 2012). Additional species generally characteristic of other ungulate hosts, like *Nematodirus skrjabini,* may also parasitize reindeer (Dikmans, 1935; Bergstrom, 1983; Lichtenfels and Pilitt, 1983; Fruetel and Lankester, 1989; Hoberg et al., 2001). Based on recent sampling in Fennoscandia and compared to historical baselines, prevalence of *Nematodirus* sp. has not changed significantly. For example, it was 16% among 115 reindeer calves a decade ago (Laaksonen et al., 2008) and 22% among 480 reindeer calves in the most recent study (Jokelainen et al., 2019).

Eggs among genera and species of nematodirines are similar and cannot be distinguished morphologically (Fig 1, B). The freeze and desiccation tolerant eggs are produced throughout winter (Fruetel, 1987; Hrabok, 2006). It appears that the epidemiology and lifecycle of these parasites in reindeer resembles patterns observed in sheep (Soulsby, 1982). Reindeer develop immunity and become highly resistant to re-infection in their second summer (Hrabok et al., 2007). However, some nematodirines have been seen in high prevalence in adult female caribou (Steele et al., 2013) and in males during rut (Fruetel, 1987; Moroni, B., unpublished data).

Capillaria spp.

Capillaria spp. (Trichocephalida: Trichuridae) are parasites of a diverse assemblage of mammals and birds. Adults are characteristically thread-like, 8–20 mm long, and in ruminants inhabit the small intestine (Soulsby, 1982). There remains some confusion and uncertainty about species identity of *Capillaria* in free-ranging ungulates, including cervids. Species of *Capillaria* have been encountered in reindeer from the Kola Peninsula and in zoo-parks from Russia (Mitskevich, 1959a). Typical eggs with symmetrical bipolar plugs (Fig. 1, C) have been observed in reindeer feces from Fennoscandia (Christensson and Rehbinder, 1975; Rehbinder and Christensson, 1977; Nordkvist et al., 1983; Oksanen et al., 1992, Hrabok et al., 2006; Laaksonen et al., 2008), from Iceland (*C. bovis*) (Gudmundsdóttir, 2006) and in a zoo-park from Germany (Markowski, 2013). These parasites shed eggs throughout the year and appear to be most abundant in the coldest winter months. Based on egg output, the parasite appears to be more common in calves (Hrabok, 2006). Species of *Capillaria* have not been reported to be associated with any specific symptoms in ruminants (Soulsby, 1982) although as documented by Wakelin and Lee (1987), heavy infection can cause enteritis and diarrhea. Little is known about this abundant reindeer parasite although it has been reported to be a dominant parasite of reindeer in zoo enclosures (Markowski, 2013). In Fennoscandia, *Capillaria* sp. prevalence was 8% among 115 reindeer calves in an earlier study (Laaksonen et al., 2008) and 9.4% among 480 reindeer calves in the most recent collections (Jokelainen et al., 2019).

Trichuris spp.

Trichuris spp. (Trichocephalida: Trichuridae), generally known as “whipworms”, are parasites inhabiting the intestines of many mammal species. They can produce an acute or chronic inflammation in the caecum. Eggs (Fig. 1, D) dispersed in feces are long-lived and resistant to a range of weather conditions. The embryonated eggs contain an infective stage larva and after ingestion by the host they hatch to establish patent infections in the definitive host. At least five species of *Trichuris* have been reported in reindeer from Russia (Mitskevich, 1959b; 1965). *Trichuris* spp. are not commonly observed in reindeer nor in moose (*Alces alces*) from Europe and are considered of no concern in wild moose (Lankester and Samuel, 2007). *Trichuris* spp. can however cause bloody diarrhea, especially in young animals (Hoeve et al., 1988) and merit attention in captive or farming situations (Clauss et al., 2002; Lankester and Samuel, 2007). In Europe, *Trichuris* spp. infections in captive moose have been associated with host aggregation during grazing on pasture and with supplementary feeding. Furthermore, these parasites may be a component of the Wasting Syndrome Complex, a condition of chronic diarrhea and body mass loss (Clauss et al., 2002; Milner et al., 2013), which is not to be confused with the prion disease Chronic Wasting Disease. In Finnish zoos, *Trichuris* sp. is a frequent cause of diarrhea in moose, and the death of one reindeer, which lived in close contact with sheep, has also been attributed to *Trichuris* sp. (Oksanen, A., unpublished data). In a recent epidemiological study, *Trichuris* sp. eggs were detected in three reindeer calves from Finland (Jokelainen et al., 2019).

Skrjabinema spp.

Commonly known as “pinworm,” *Skrjabinema* is a genus within the family Oxyuridae. The life cycle is direct, and infection occurs through the ingestion of eggs containing larvae, which are deposited on the perianal skin by females (Sapozhnikov, 1969). The eggs are easily identified based on their asymmetric shape (Oksanen, 1999). The adults live in the caecum of ruminants.

Skrjabinema spp. are not regarded as pathogenic (Soulsby, 1982) but occasionally are observed in sheep and goats and free-ranging ungulates (Borgsteede and Dercksen, 1996). *Skrjabinema tarandi* has been reported in reindeer from Fennoscandia (Josefsen et al., 2014). In a recent epidemiological study, eggs of *Skrjabinema* sp. were detected in one reindeer from Finland (Jokelainen et al, 2019).

2.3 Gastrointestinal cestodes

Reindeer are definitive hosts of a number of species of cestodes of the family Anoplocephalidae. These parasites are hermaphroditic flatworms with complex lifecycles. As adults, ranging up to several meters in length, they live in the intestines of reindeer. Tapeworm segments (proglottids) are passed in the feces and eggs are then ingested by arthropod intermediate hosts (oribatid mites, insects or springtails (Collembola)), (Samuel and Gray, 1974; Soulsby, 1983; Elliott, 1986; Kozlov, 1986; Denegri, 1989; Xiao and Herd, 1992), where they undergo temperature-dependent development (Narsapur and Prokopic, 1979) to the cysticercoid stage. Reindeer are infected when they ingest infected arthropods from pastures.

Cestodes are found across most of the reindeer range in Fennoscandia. Species that have been reported across the Holarctic include *Avitellina arctica* in caribou from Canada (Gibbs, 1960), *Moniezia benedeni*, *M. taimyrica*, and *M. rangiferina* in reindeer from Russia, Norway, and South Georgia Island, and possibly a species of *Thysanosoma* (Mitskevich, 1960; Semenova, 1967; Zelinskii, 1973; Pryadko, 1976; Leader-Williams, 1980; Bye, 1985).

Tapeworms of reindeer have been little studied in Fennoscandia. In Svalbard, 6 of 16 (43%) calves had cestodes (Bye, 1985). In Fennoscandia, the prevalence of *Moniezia* sp. egg shedding was 18% among 115 reindeer calves in an earlier study (Laaksonen et al., 2008), and statistically significantly higher, 28%, among 480 reindeer calves in a more recent study (Jokelainen et al., 2019).

Recent molecular phylogenetic analyses by Haukisalmi et al. (2018) revealed that specimens of *Moniezia* from moose and reindeer were not conspecific with those species commonly reported in domestic ruminants. These conclusions indicate that identifications of *Moniezia* spp. in northern cervids as either *M. expansa* or *M. benedeni* are likely to be incorrect. Further, at least two of the putative species-level taxa found parasitizing moose and reindeer from the Holarctic have not been previously recognized. These findings demonstrate a species complex and challenge the results of earlier studies concerning the diversity and ecology of *Moniezia* spp. in northern cervids. Eggs in feces can be identified to the generic level morphologically, but not reliably to species (Fig. 1, E).

Very little is known of the impact of cestodes in reindeer. These tapeworms appear most common in young animals (Kirilenko, 1975; Soulsby, 1982; Bye, 1985). There is little doubt that infections of low intensity are of little importance (Low, 1976; Rehbinder and Christensson, 1977; Soulsby, 1982). Heavy infections, with a solid mass of tapeworms in the intestine, can cause clinical signs including ill health, weight loss, and diarrhea (Hellesnes, 1935; Polyanskaya, 1961; Kirilenko, 1975; Laaksonen, 2016).

3. Discussion

Our review provides an overview of the available data regarding gastrointestinal parasites of reindeer in Fennoscandia, where host-parasite systems have the potential to be strongly influenced by outcomes of climate warming and environmental change. These impacts have already been clearly observed as a major influence on the distribution of vector-borne parasites and expanding disease in Finland, and among an assemblage of filarioid nematodes that is of direct concern for semi-domestic reindeer (e.g., Laaksonen et al., 2007; 2010; 2017). Field-based explorations of parasite development for an array of gastrointestinal nematodes, tapeworms and protozoans (e.g., temperature and moisture, resilience and the parameters that can limit, control or facilitate the persistence and dissemination of parasite infections) are increasingly important given the pace of environmental change at high latitudes (Hoberg et al., 2017). Baselines and monitoring are essential and may become critical with a potential failure of antiparasitic interventions on which we have relied for parasite control. This apparent and potential convergence or synergy for ameliorating environmental conditions may favor parasite transmission. For example, the increase in proportion of reindeer calves shedding eggs of strongylids has increased from historical estimates and significantly within a decade recently (Laaksonen et al., 2008; Jokelainen et al., 2019). Observations like this would merit further studies to evaluate whether they reflect changing management or environmental conditions.

Furthermore, concerns of potential loss of effective control measures demonstrate a need for targeted monitoring to reveal changes in parasite diversity and distribution, and emergence of disease or related economic impacts that can directly influence food sustainability and availability (Brooks et al., 2014; Hoberg and Zarlenga, 2016; Laaksonen et al., 2017). Moreover, potential changes in host populations, including free-ranging wildlife, semidomesticated animals and domestic animals, and in their parasitic fauna, should be taken into account in monitoring and research efforts. The interface between wild, semidomesticated and domestic animals merits more attention, and transdisciplinar collaboration and intersectoral communication should be encouraged. The situation in Fennoscandia is changing, and establishing monitoring targeting suitable indicator parasites, e.g., monitoring of the gastrointestinal parasites strongylids and *Eimeria* sp. in reindeer (Jokelainen et al., 2019), would ensure that reindeer management stays informed and can adapt.

From our review of the literature, covering both historical baseline data and recent field-based studies, it is evident that the balance between reindeer and their gastrointestinal parasites, especially nematodes, requires ongoing monitoring and further studies. Pertinent are the effects to reindeer health and welfare, dynamics of the parasites in reindeer and on pasture, their lifecycles, potential adaption to rapidly changing environmental conditions in the Arctic and the possible development of resistance against the most widely used antiparasitic, ivermectin. Molecular methods and phylogenetic studies are welcomed to confirm and challenge previous knowledge that is largely based on morphology. The interaction of climate in determining the potential geographic range of some parasites (through limitations on development or resilience on grazing lands), and the potential for origins and spread of antiparasitic resistance are a particular concern and represent a broader generality for ungulate parasite systems even in the temperate-boreal zone (Hoberg et al., 2008). Several aspects, including economics as well as timing, extent and targeting of the antiparasitic application and use of other nonchemical means of prevention should be identified and evaluated (Haider et al., 2018; Jokelainen et al., 2019).

Conflict of interest

None.

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References

Abbas, B., Post, G., 1980. Experimental coccidiosis in mule deer fawns. J. Wildl. Dis. 16, 565–570.

Albon, S.D., Stien, A., Irvine, R.J., Langvatn, R., Ropstad, E., Halvorsen, O., 2002. The role of parasites in the dynamics of a reindeer population. Proc. Biol. Sci. 269, 1625–1632.

Armour, J., Duncan, M., 1987. Arrested larval development in cattle nematodes. Parasitol. Today, 3, 171–176.

Arneberg, P., Folstad, I., Karter, A., 1996. Gastrointestinal nematodes depress food intake in naturally infected reindeer. Parasitology 112, 213–219.

Bergstrom, R.C., 1983. Occurrence of *Nematodirella* sp. (Nematoda: Trichostrongyloidea) in domestic sheep (*Ovis aries*) of Wyoming. Proc. Helminthol. Soc. Wash. 50, 335–336.

Borgsteede, F.H, Dercksen, D.P., 1996. Coccidial and helminth infections in goats kept indoors in the Netherlands. Vet. Parasitol. 61, 321–326.

Brooks, D.R., Hoberg, E.P., Gardner, S.L., Boeger, W., Galbreath, K.E., Herczeg, D., Mejía-Madrid, H.H., Racz, E., Tsogtsaikhan Dursahinhan, A., 2014. Finding them before they find us: Informatics, parasites and environments in accelerating climate change. Comp. Parasitol. 81, 155–164.

Bye, K., 1985. Cestodes of reindeer (*Rangifer tarandus platyrhynchus* Vrolik) on the Arctic islands of Svalbard. Can. J. Zool. 63, 2885–2887.

Bye, K., 1987. Abomasal nematodes from three Norwegian wild reindeer populations. Can. J. Zool. 65, 677–680.

Bye, K., Halvorsen, O., 1983. Abomasal nematodes of the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik) J. Wildl. Dis. 19,101–105.

Bye, K., Halvorsen, O., Nilssen, K., 1987. Immigration and regional distribution of abomasal nematodes of Svalbard reindeer. J. Biogeogr. 14, 451–458.

Carlsson, A.M., Irvine, R.J., Wilson, K., Coulson, S.J., 2013. Adaptations to the Arctic: low-temperature development and cold tolerance in the free-living stages of a parasitic nematode from Svalbard. Polar Biology 36, 997–1005.

Carlsson, A.M., Mastromonaco, G., Vandervalk, E., Kutz, S., 2016. Parasites, stress and reindeer: infection with abomasal nematodes is not associated with elevated glucocorticoid levels in hair or faeces. Conserv Physiol. 4, cow058.

Christensson, D., Rehbinder, C. 1975. Parasiter hos renkalv - en träkprövsundersökning. Nord. Vet. Med. 27, 496–498. (in Norwegian)

Clauss, M., Kienzle, E., Wiesner, H., 2002. Importance of the wasting syndrome complex in captive moose (*Alces alces*). Zoobiology 21, 499–506.

Conloque, G.C., Foreyt W.J., 1984. Experimental infections of *Eimeria mccordocki* (Protozoa, Eimeriidae) in white-tailed deer. J. Wildl. Dis. 1, 291–300.

Dau J., Eimeria. 1981. In: Dietrich R.A. (Ed.), Alaskan Wildlife Diseases. Univ of Alaska, Fairbanks, pp. 171–173.

Denegri, G.M., 1989. New potential intermediate host of *Moniezia expansa* Rudolphi, 1810, in Argentina. Vet. Parasitol. 33, 191–194.

Dikmans, G., 1935. A note on the identity of *Nematodirus tarandi* Hadwen, 1922, and *Nematodirus skrjabini Mitzkewitsch*, 1929 (Nematoda: Trichostrongylidae). Proc. Helminthol. Soc. Wash. 2, 56.

Drózdz, J., 1995. Polymorphism in the Ostertagiinae Lopez-Neyra, 1947 and comments on the systematics of these nematodes. Systematic Parasitology 32, 91–99.

Elliott, D.C., 1986. Tapeworm (*Moniezia expansa*) and its effect on sheep production: the evidence reviewed. N. Z. Vet. J. 34, 61–65.

Foreyt, W.J., Lagerquist, J.E., 1994. Experimental infections of *Eimeria wabiti* and *E. zuernii*-like oocysts in Rocky Mountain elk (*Cervus elaphus*) calves. J. Wildl. Dis. 3, 446–449.

Fruetel, M., 1987. The biology of the gastro-intestinal helminths of woodland and barren-ground caribou (*Rangifer tarandus*), Thesis, Lakehead University.

Fruetel, M., Lankester, M.W.,1988. *Nematodirella alcidis* (Nematoda: Trichostrongyloidea) in moose of northwestern Ontario. Alces 24, 159–163.

Fruetel, M., Lankester, M.W., 1989. Gastrointestinal helminths of woodland and barren ground caribou (*Rangifer tarandus*) in Canada, with key to species. Can. J. Zool. 67, 2253–2269.

Gibbs, H.C., 1960. A redescription of Avitellina arctica Kolmakov, 1938 (Anoplocephalidae: Thysanosominae), from *Rangifer arcticus arcticus* in northern Canada. J. Parasitol. 46, 624–628.

Gudmundsdóttir, B., 2006. Parasites of reindeer (*Rangifer tarandus*) in Iceland. Master of Science degree. Faculty of Medicine, University of Iceland, 100 pp. (in Icelandic)

Gudmundsdóttir, B., Skirnisson, K., 2005. Description of a new *Eimeria* species and redescription of *Eimeria mayeri* (Protozoa: Eimeriidae) from wild reindeer (*Rangifer tarandus*) in Iceland. J. Parasitol. 91, 353–357.

Gudmundsdóttir, B., Skirnisson, K., 2006. The third newly discovered *Eimeria* species (Protozoa:Eimeriidae) described from wild reindeer, *Rangifer tarandus*, in Iceland. Parasitol. Res. 99, 659–662.

Haider, N., Laaksonen, S., Kjær, L.J., Oksanen, A., Bødker, R., 2018. The annual, temporal and spatial pattern of *Setaria tundra* outbreaks in Finnish reindeer: a mechanistic transmission model approach. Parasit Vectors, 11, 565.

Halvorsen, O., 1986. Epidemiology of reindeer parasites. Parasitol. Today 2, 334–339.

Halvorsen, O., Stien, A., Irvine, J., Langvatn, R., Albon, S., 1999. Evidence for continued transmission of parasitic nematodes in reindeer during Arctic winter. Int. J. Parasitol. 29, 567–579.

Haukisalmi, V., Laaksonen, S., Oksanen, A., Beckmen, K., Halajian, A., Yanagida, T., Nakao, M., 2018. Molecular taxonomy and subgeneric classification of tapeworms of the genus *Moniezia* Blanchard, 1891 (Cestoda, Anoplocephalidae) in northern cervids (*Alces* and *Rangifer*). Parasitol. Int. 67, 218–224.

Hellesnes, P., Rensnyltere. 1935. Nork Veterinärtidssskrift 47, 117–137;194–204. (in Norwegian)

Hoar, B., Oakley, M., Farnell, R., Kutz, S., 2009. Biodiversity and springtime patterns of egg production and development for parasites of the Chisana Caribou herd, Yukon Territory, Canada. Rangifer 29, 25–37.

Hoar, B., Ruckstuhl K., Kutz S., 2012. Development and availability of the free-living stages of *Ostertagia gruehneri*, an abomasal parasite of barrenground caribou (*Rangifer tarandus groenlandicus*), on the Canadian tundra. Parasitology 139, 1093–1100.

Hoberg, E.P., Kocan, A.A., Rickard, L.G., 2001. Gastrointestinal strongyles in wild ruminants. In: Samuel, W.M., Pybus, M.J., Kocan, A.A. (Eds.), Parasitic Diseases of Wild Mammals. Iowa State University Press, Ames, pp. 193–220.

Hoberg, E.P., Monsen, K.J., Kutz, S., Blouin, M.S., 1999. Structure, biodiversity and historical biogeography of nematode faunas in Holarctic ruminants: Morphological and molecular diagnoses for *Teladorsagia boreoarcticus* n. sp. (Nematoda: Ostertagiinae) a dimorphic cryptic species in muskoxen (*Ovibos moschatus*). J. Parasitol. 85, 910–934.

Hoberg, E.P., Polley, L., Jenkins, E.J., Kutz, S.J., 2008. Pathogens of domestic and free-ranging ungulates: Global climate change in temperate to boreal latitudes across North America. Rev. Off. Int. Épizoot. 27, 511–528.

Hoberg, E.P., Abrams, A., Pilitt, P.A., Jenkins, E.J., 2012. Discovery and description of a new trichostrongyloid species (Nematoda: Ostertagiinae), abomasal parasites in mountain goat, *Oreamnos americanus* from the western Cordillera of North America. J. Parasitol. 98, 817–846.

Hoberg, E.P., Zarlenga, D.S., 2016. Evolution and biogeography of *Haemonchus contortus*, linking faunal dynamics in space and time. *Haemonchus contortus* and Haemonchosis: Past, Present and Future Trends. In: Gasser, R.B., von Samson-Himmelstjerna, G. (Eds.), Adv. Parasitol. 93, 1–30.

Hoberg, E.P., Cook, J.A., Agosta, S.J., Boeger, W., Galbreath, K.E., Laaksonen, S., Kutz, S.J., Brooks, D.R., 2017. Arctic systems in the Quaternary: Ecological collision, faunal mosaics and the consequences of wobbling climate. J. Helminthol. 91, 409–421.

Hoeve, J., Joachim, D.G., Addison, E.M., 1988. Parasites of Moose (*Alces alces*) from an Agricultural Area of Eastern Ontario. J. Wildl. Dis. 24, 371–374.

Horstkotte, T., Aikio A., 2017. Reindeer husbandry under global change in the tundra region of northern Fennoscandia. In: Käyhkö, J., Horstkotte, T. (Eds.), Publications from the department of geography and geology, University of Turku. No 1. University of Turku, Turku, pp. 19–28

Hrabok, J.T., 2006. Nematode Parasites of Reindeer in Fennoscandia, Population Dynamics, Anthelmintic Control and its Environmental Impact. Doctoral thesis, Swedish University of Agricultural Sciences, Uppsala, 52 pp.

Hrabok, J.T., Oksanen, A., Nieminen, M., Waller, P.J., 2006. Population dynamics of nematode parasites of reindeer in the sub-arctic. Vet. Parasitol. 142, 301–311.

Hrabok, J.T., Oksanen, A., Nieminen, M., Waller, P.J., 2007. Prevalence of gastrointestinal nematodes in winter slaughtered reindeer of northern Finland. Rangifer 27, 133–139.

Hughes, J., Albon, S.D., Irvine, R.J., Woodin, S., 2009. Is there a cost of parasites to caribou? Parasitology 136, 253–265.

Irvine, R., Stien, A., Halvorsen, O., Langvatn, R., Albon, S., 2000. Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Parasitology 120, 297–311.

Jokelainen, P., Moroni, B., Hoberg, E., Oksanen, A., Laaksonen, S. 2019. Gastrointestinal parasites in reindeer (*Rangifer tarandus tarandus*) calves from Fennoscandia: An epidemiological study. Vet. Parasitol. Reg. Stud. Rep. 16, 100277.

Josefsen, T.D., Oksanen, A., Gjerde, B., 2014. Parasiter hos rein I Fennoskandia – en oversikt. Norsk veterinærtidsskrift, 2, 185–201. (in Norwegian)

Kirilenko, A.V., 1975. Avitellina arctica in rangifer tarandus. Veterinariya 7, 58–59. (in Russian)

Klesius, P.H., 1993. Regulation of immunity to *Ostertagia ostertagi*. Vet. Parasitol. 46, 63–69.

Kozlov, D.P., 1986. Collembola, possible intermediate hosts of (Cestoda, Anoplocephalata). Parazitologiia 20(1), 73–74.

Kutz, S.J., Ducrocq, J., Verocai, G.G., Hoar, B.M., Colwell, D.D., Beckmen, K.B., Polley, L., Elkin, B.T., Hoberg, E.P., 2012. Parasites in ungulates of Arctic North America and

Greenland: a view of contemporary diversity, ecology, and impact in a world under change. Adv. Parasitol. 79, 99–252.

Laaksonen, S., 2016. Tunne poro – poron sairaudet ja terveydenhuolto. Livonia print, Riga, 375 pp. (in Finnish)

Laaksonen, S., Kuusela, J., Nikander, S., Nylund, M., Oksanen, A., 2007. Parasitic peritonitis outbreak in reindeer (*Rangifer tarandus tarandus*) in Finland, Vet. Rec. 160, 835–841.

Laaksonen, S., Oksanen, O., Orro, T., Norberg, H., Nieminen, M., Sukura, A., 2008. Efficacy of different treatment regimes against setariosis (*Setaria tundra*, Nematoda: Filarioidea) and associated peritonitis in reindeer. Acta Vet. Scand. 50, 49.

Laaksonen, S., Pusenius, J., Kumpula, J., Venäläinen, A., Kortet, R., Oksanen, A., Hoberg, E., 2010. Climate change promotes the emergence of serious disease outbreaks for Filarioid nematodes. Ecohealth 1, 7–13.

Laaksonen, S., Oksanen, A., Kutz, S., Jokelainen, P., Holma-Suutari, A., Hoberg, E., 2017. Filarioid nematodes, threat to arctic food safety and security – Bioinvasion of vector-borne filaroid nematodes in the arctic and boreal ecosystems. In: Paulsen, P., Bauer, A., Smulders, F.J.M. (Eds.), Game meat hygiene: Food safety and security.

Lankester, M.W., Samuel, W.M., 2007. Pests, parasites and diseases. In: Franzmann, A.W., Schwartz, C.C. (Eds.), Ecology and Management of the North American moose (2. ed.). University press of Colorado, Colorado.

Leader-Williams, N., 1980. Observations on the internal parasites of reindeer introduced into South Georgia. Vet. Rec. 107, 393–395.

Lichtenfels, J., Pilitt, P., 1983. Cuticular ridge patterns of *Nematodirella* (Nematoda: Trichostrongyloidea) of North American ruminants, with a key to species. Systematic Parasitology 5, 271–285.

Lloyd, S., Soulsby, E.J.L., 1987. Immunobiology of gastrointestinal nematodes of ruminants. In: Soulsby, E.J.L. (Ed.), Immune responses in parasitic infections: immunology, immunopathology and immunoprophylaxis. Volume I Nematodes. CRC Press, Boca Raton, pp. 1–41.

Low, W.A., 1976. Parasites of woodland caribou in Tweedsmuir Provincial Park, British Columbia. Canadian Field–Naturalist 90, 189–191.

Manninen, S.M., Thamsborg, S.M., Laaksonen, S., Oksanen, A., 2014. The reindeer abomasal nematode (*Ostertagia gruehneri*) is naturally transmitted to sheep when sharing pastures. Parasitol. Res. 113, 4033–4038.

Markowski, S., 2013. Tierart- und erregerspezifische Maßnahmen zur Optimierung des Gesundheitsmanagements für nordamerikanische Säugetiere in Zoologischen Gärten. Dissertation. Hannover, Tierärztliche Hochschule. (in German)

Milner, J.M., Sari J.W., Laaksonen, S., Oksanen, A., 2013. Gastrointestinal nematodes of moose (*Alces alces*) in relation to supplementary feeding. J. Wildl. Dis. 49, 69–79.

Mitskevich, V.Y., 1959a. *Capillaria* spp. in reindeer (*Rangifer tarandi*). Trudi Voronezhskogo Zoovetinstituta. 16 pp. 263–275.

Mitskevich, V.Y., 1959b. *Trichuris* spp. from reindeer. Sbornik Rabot 22 pp. 69–78.

Mitskevich, V.Y., 1960. *Moniezia* infections of reindeer. Tezisi Dokl. Nauchnoi Konf. Vses. Obshch. Gelm. pp. 89–90.

Mitskevich, V.Y., 1965. *Trichuris* n. sp. from reindeer. Mater. nauch. Konf. (XIV) pp. 54–55.

Narsapur, V.S., Prokopic, J., 1979. The influence of temperature on the development of *Moniezia expansa* (Rudolphi 1810) in oribatid mites. Folia Parasitologica 26, 239–243.

Nikander, S., 1986. Coccidier hos ren. Rangifer, No 1 Appendix, 88. (in Swedish)

Nikander, S., 1988. Abomasal helminths of cervids in Finland. Nordic Congress on Game Research. pp. 44.

Nordkvist, M., Rehbinder, C., Christensson, D., Rönnbäck, C., 1983. A comparative study on the efficacy of four anthelmintics on some important reindeer parasites. Rangifer 3, 19–38.

Oksanen, A., 1999. Endectocide treatment of the reindeer. Thesis. Rangifer, Special Issue 11, 118 pp.

Oksanen, A., Nieminen, M., Soveri, T., Kumpula, K., 1992. Oral and parenteral administration of ivermectin to reindeer. Vet. Parasitol. 41, 241–247.

Oksanen, A, Nieminen, M., Soveri, T., Kumpula, K., Heiskari, U., Kuloharju, V., 1990. The establishment of parasites in reindeer calves. Rangifer, Special issue 5, 20–22.

Pellérdy, L.P., 1974. Coccidia and coccidiosis. Akadémiai Kiado, Budapest, Hungary.

Polyanskaya, M.V., 1961. Moniezia infestation in reindeer calves. Veterinaria 7, 46–47.

Pryadko, E.I., 1976. Gel'minty olenej. Izd. Nauka Kazakh. SSR, Alma-Ata. (in Russian).

Rehbinder, C., Christensson, D., 1977. The presence of gastro-intestinal parasites in autumn-slaughtered reindeer bulls. Nord. Vet. Med. 29, 556–557.

Rehbinder, C., von Szokolay, P., 1978. The presence of gastric parasites in winter slaughtered reindeer. Nord. Vet. Med. 30, 214–216.

Samuel, W.M., Gray, D.R., 1974. Parasitic infection in muskoxen. J. Wildl. Manag. 38, 775–782.

Sapozhnikov, G.I., 1969. The life-cycle of *Skrjabinema ovis* (Skryabin, 1915). Trudy vsesoyuznogo Instituta Gel'mintologii 15, 267–274.

Semenova, N.S., 1967. Study of Moniezia (Moniezia) taimyrica Semenova, 1967 in reindeer. Materialy Nauchnykh Konferentsii Vsesoyuznogo Obshchestva Gel'-mintologov, 1971–1972, 25, 199–202. (in Russian)

Skirnisson, K., Cuyler, C., 2016. A new *Eimeria* species (Protozoa: Eimeriidae) from caribou in Ameralik, West Greenland. Parasitol. Res. 115, 1611–1615.

Soulsby, E.J.L., 1982. Helminths, arthropods and protozoa of domestic animals. 7th ed. Bailliere Tindall., London, pp. 809.

Steele, J.F., 2013. The devil's in the diversity: divergent parasite faunas and their impacts on body condition in two Greenland caribou populations. MSc thesis, University of Calgary, Calgary, Alberta, Canada.

Steele, J.F., Orsel, K., Cuyler, C., Hoberg, E.P., Schmidt, N.M., Kutz, S.J., 2013. Divergent parasite faunas in adjacent populations of west Greenland caribou: Natural and anthropogenic influences on diversity. Int. J. Parasitol. Parasites Wildl. 2, 197–202.

Stien, A., Irvine, R., Ropstad, E., Halvorsen, O., Langvatn, R., Albon, S., 2002a. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. J. Anim. Ecol. 71, 937–945.

Stien, A., Irvine, R.J., Langvatn, R., Albon, S.D., Halvorsen, O., 2002b. The population dynamics of *Ostertagia gruehneri* in reindeer: a model for the seasonal and intensity dependent variation in nematode fecundity. Int. J. Parasitol. 32, 991–996.

Svensson, C., 1995. Survival of oocysts of *Eimeria alabamensis* on pastures under different climatic conditions in Sweden. Acta Vet. Scand. 36, 9–20.

Sykes, A.R., 1987. Endoparasites and herbivore nutrition. In: Hacker, J.B., Ternouth, J.H. (Eds.), The nutrition of herbivores. Proceedings of the second International Symposium on the Nutrition of Herbivores, pp. 211–232.

Tryland M., Kutz, S.J. (Eds.), 2018. Reindeer and Caribou: Health and Disease. First Edition. CRC Press, Boca Raton, 534 pp.

Wakelin, D., Lee T.D.G., 1987. Immunobiology of Trichuris and Capillaria infections. In: Soulsby, E.J.L. (Ed.), Immune responses in parasitic infections: Immunology, immunopathology and immunoprophylaxis. Volume I Nematodes. CRC Press, Boca Raton, pp. 61–88.

Xiao, L., Herd, R.P., 1992. Infectivity of *Moniezia benedeni* and *Moniezia expansa* to oribatid mites from Ohio and Georgia. Vet. Parasitol. 45, 101–110.

Yakimoff, W.L., Sokoloff, I.I., Matschoulsky, S.N., 1936. Über die Kokzidien des Rentieres. Berl Tierarztl Wochenschr 52, 535–538. (in German)

Yakimoff, W.L., Matschoulsky, S.N., Spatansky, O.A., 1937. Weitere Untersuchungen über Kokzidiose bei den Rentieren. Berl Tierarztl Wochenschr 53, 322. (in German)

Yakimoff, W.L., Matschoulsky, S.N., Spatansky, O.A., 1939. On a new coccidium from reindeer, *Eimeria arctica* n. sp. J. R. Microsc. Soc. 59, 30–31.

Zelinskii, L.M., 1973. Identification of *Moniezia rangiferina* from reindeer on the Kamchatka Peninsula, Siberia, USSR. Sbornik Rabot. Leningradskii Veterinarnyi Institut 32, 43–44.

Figure legends

Figure 1. Eggs and oocysts of parasites of reindeer (*Rangifer tarandus tarandus*): strongylid (A), *Nematodirus* sp. (B), *Capillaria* sp. (C), *Trichuris* sp. (D), *Moniezia* sp. (E), *Eimeria* sp. (F). Scale bars 20 µm.

Highlights

- Infections with gastrointestinal parasites are common in reindeer
- Knowledge gaps are several, and baseline data are needed
- The balance between reindeer and their parasites needs careful monitoring

Conflict of Interest.
None.

Ethical Statement
No ethical concerns.